THE STATUS OF NITROGEN IN THE HAWKESBURY SANDSTONE SOILS AND THEIR PLANT COMMUNITIES IN THE SYDNEY DISTRICT. I.

The Significance and Level of Nitrogen.

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(Plate x; one Text-figure.)

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Synopsis.

The soils derived from Hawkesbury Sandstone in the Sydney district are of low fertility. Phosphorus and nitrogen are the chief limiting nutrients. The level of nitrogen in the parent rock, the soils and the plant material of these communities is described. Low concentrations prevail throughout, but increase from approximately 180 p.p.m. in the rock to the order of 600 p.p.m. in the surface soils. The soils are acid, pH 4·5-5·0, with high carbon-nitrogen ratios (18-49). Consequently, the level of available nitrogen is extremely low. The nitrogen content of much of the fresh leaf material is only about 7,000 p.p.m., but members of the Leguminosae and Casuarinaceae average 12,000 p.p.m. Similarly, seed of legumes and *Casuarina* L. contains at least four times the amount of nitrogen found in other species. Freshly fallen leaf litter contains a large percentage of the nitrogen content of mature leaves.

Introduction.

The natural plant communities of the Sydney district attract attention because of the mosaic of formations which occur and the distinctive and sclerophyllous character of many of their members. The majority of the species belong to the endemic Australian element, with Indo-Malayan representatives occurring only in restricted areas of improved environmental conditions. Trees and woody shrubs predominate, herbs and grasses being less conspicuous. There is a great diversity of floral type and leaf form.

Over a period of years several workers have been engaged in investigations of a number of aspects of the nature of these communities. These include floristic and structural descriptions, physiological studies, nutrient levels and requirements, anatomical, morphological and cytological investigations, and studies on the microflora and fauna involved in *Casuarina* litter decomposition. The present series of papers will make a further contribution to the knowledge already accumulated. Much detailed information, especially autecological studies, is still lacking; but when the communities have been characterized in sufficient detail, a synthesis of the various contributions should illustrate the basic chemical, physical and biological factors which are interacting to produce the resultant mechanism of the ecosystem. To date, reports of such syntheses are very few. Platt's (1951) ecological study of the Mid-Appalachian shale barrens forms a notable exception.

Since detailed descriptions of the associations and their habitat have been made by Pidgeon (1937, 1938, 1940, 1942), only a brief account will be included here.

There are three geological formations within the district, all of which are Triassic sediments. They are the Narrabeen Group (shales and sandstones), the Hawkesbury Sandstone and the Wianamatta Group (shales and sandstones), as described by Hanlon, Joplin and Noakes (1952).

Apart from several widely scattered outliers, the uppermost division of the Triassic, the Wianamatta Group, still remains in only the Sydney Plains, an area of approximately 35 by 50 square miles.

The Narrabeen Group outcrops cover a still smaller area near the coastal region to the north and south of Sydney.

A deeply dissected plateau region composed chiefly of Hawkesbury Sandstone extends to the north, south and west of Sydney. The horizontal bedding and resistant nature of the sandstone are responsible for the typical physiographic characters of the plateaux—the flat-topped divides and the steep gullies. This deposit consists predominantly of quartz grains, and the analyses given in the N.S.W. Mines Department's Annual Reports (1902, 1905, 1906, 1914, 1915, 1922) show very low levels of the elements required for plant nutrition. Lenticular beds of shale, generally only small, are scattered fairly frequently throughout the sandstone. The soils derived from it are highly siliceous with aluminous or ferriferous clay as the cementing agent and are light-coloured sandy loams. The youthful physiography of the plateaux and the comparative hardness of the rock strata have caused the development of shallow and immature soils. Outcrops of rock are very frequent in all types of communities. It is only on gentle slopes of gullies and in restricted sheltered areas of the plateaux that soil development proceeds to any depth. The soils are much lighter in texture, of a lower water-retaining capacity, and of less productivity than those derived from the Wianamatta and Narrabeen shales. They support the most sclerophyllous species which form a moderately dense cover.

There are two major habitats in which primary plant succession may occur on Hawkesbury Sandstone—the outcrops of the sandstone itself and the beach sand dunes which have been largely derived from it. These present very different media for plant growth.

The sandstone weathers slowly. Algae and lichens—crustose, foliose and fruticose forms in association with mosses—are often found on the rock surfaces. When the mosses are well established and the soil is a few inches deep, herbs and shrubs are found growing in the moss mats. The soil pH averages 4·5. The pioneer stages may be seen on rock outcrops scattered throughout the more advanced communities. From this stage a heath of sclerophyllous, evergreen shrubs is developed. Apart from changes in evaporation, temperature, light and soil in the early stages of the succession, changes providing increased shelter are all important for development from the heath stage. Progression beyond this point is determined by physical features of the environment, such as exposure, drainage, depth of soil and topography, which in turn influence the chemical factors as the supply of nutrients and water. Scrub and tree scrub merging into scrub forests* of various heights, or dry sclerophyll forest may be formed. Transitions from dry to wet sclerophyll forest are found in more favourable situations. The sclerophyll forests are dominated by various associations of *Eucalyptus* L'Hérit.† species. On Wianamatta Shale tall woodland and wet sclerophyll forests occur, and on the Narrabeen Series the wet sclerophyll or rainforest is developed. The different formations are characterized by different species. This distribution pattern is very marked and constant. Such great differences in vegetation type reflect equally great differences in environment.

Where drainage conditions are poor on Hawkesbury Sandstone, either a sedge or shrub swamp is developed, dependent on moisture conditions. The sedge swamps require the higher water level. The development of swamps is due, in some instances, to cupping of the sandstone, and in other cases to the presence of an impervious shale lens in the sandstone. The swamps are found on the uplands, and occur quite frequently. They are, however, usually of limited area.

The sand dunes have a high calcium carbonate and sodium chloride content and are of high pH value (8·0). The soil depth, moderate phosphate content and deficiency of organic matter also distinguish them from the soil formed in the lithosere. Behind the sand binding species as the grasses and mat plants, *Acacia sophorae* (Labill.) R. Br. forms a well defined zone and is the first of the shrubs to appear in the succession. It occurs at the back of the first dune, where organic matter is still very low. Other shrub species, such as *Leptospermum* Forst. & f. and *Banksia* L.f., form dense thickets where soil organic matter has increased and the pH fallen below neutrality, due to the removal of the calcium carbonate by leaching. This stage is followed by the mixed

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* In terms of the glossary of Beadle and Costin (1952), these subformations should more correctly be named shrub woodlands. However, to facilitate comparison with Pidgeon's descriptions of the sandstone communities, her nomenclature has been retained.

† The names and authorities of all species have been checked at the National Herbarium, Sydney.

Eucalyptus scrub forest, similar to that developed in the lithosere. Photographic records of all of these communities appear in Pidgeon's accounts.

A number of factors have been suggested as contributors to the development of xeromorphy in leaf tissue—such as lack of water, lack of nutrients and high light intensities (Shields, 1950).

Despite an average annual rainfall ranging from 35″ to 50″ throughout the area, it was thought originally that, owing to the very sandy nature of the sandstone soils, and consequently their low water retaining capacity, lack of water was the factor responsible for the development of the xeromorphic nature of the vegetation.

Hutton (1949) grew a typical xeromorphic representative, *Hakea teretifolia* (Salisb.) J. Britt., in natural soil, without the addition of any nutrients, under glasshouse conditions. The interaction effect of two light and two water levels was studied. Significant differences in the dry weight of the plants in each of the four treatments were noted. Differences in morphological and anatomical features of the leaves were also significant. Low water conditions also caused some marked changes in the chemical composition of the plants.

A lack of combined nitrogen or other mineral elements was also considered relevant. Work in this field has shown that the supply of nutrient elements is of great significance, both in the modification of leaf form and also in the distribution of the communities throughout the whole area (Beadle, 1953, 1954).

Pidgeon (1938, 1940, 1942) considered that the distribution of the various formations was dependent on the moisture content of the soils.

Beadle (1954) has criticized Pidgeon's views and has presented evidence to show the importance of phosphorus in determining the distribution of the formations. Beadle's analyses of parent material (unpublished data) and leaves (1954) show that phosphorus is at markedly different levels in the various formations.

As yet, however, a critical investigation of the effects produced by the interaction of phosphorus and water, both of which apparently play important roles in these communities, still awaits attention. Fertilizer trials carried out in the field where water will be at its normal level, in addition to further glasshouse investigations, should prove very enlightening.

Addition of phosphorus to Hawkesbury Sandstone soil strongly stimulates plant growth, but a nitrogen deficiency soon becomes evident. An investigation of the status of nitrogen in these communities was therefore begun.

Apart from the significance of nitrogen in this particular instance, it would be of interest to account for the development of nitrogen in a plant community. While the literature dealing with the various aspects of the nitrogen cycle is voluminous, the nitrogen sources, levels, and requirements of plant communities have received little attention, except in the case of crop plants.

The need for an investigation into the source of nitrogen for plant growth in White Sands, New Mexico, was pointed out by Emerson (1935). Total nitrate and nitrite in sand taken from the immediate vicinity of roots where vegetation was relatively luxuriant was reported to be 8 p.p.m. N. Shields (1953) indicated that she intended to undertake this project.

Beadle and Tchan (1955) have begun similar investigations in the semi-arid plant communities of western New South Wales.

Unlike other mineral nutrients whose supply in a community is primarily determined by the level found in the parent material, the possible pathways for the entry of nitrogen into a plant community are many.

While all mineral nutrients are of importance, nitrogen may be considered a "key" element in a plant community. Its nitrogen content is a fairly accurate index of productivity. This is so because, in order to accumulate nitrogen, it is necessary for soil conditions to be favourable for the growth of plants and microorganisms. This growth in turn involves at least a moderate supply of all essential plant food elements, a not unfavourable soil reaction and drainage conditions, and a reasonable amount of precipitation.

Nutrient Deficiencies of Hawkesbury Sandstone Soils.

The low productivity of the soils from an agricultural viewpoint has long been recognized (Jensen, 1914). The following glasshouse experiments illustrate the nature and extent of the nutrient deficiencies.

The soils were chosen from low scrub forest and from shrub swamp communities. The *Eucalyptus* forest is the typical and most widely spread community on the sandstone; but the swamp soil was included, despite the limited occurrence of swamps, because of its higher nitrogen and organic matter content.

Methods.

The procedure in the preparation of all glasshouse experiments was as follows:

Large soil samples were collected from typical community types to a depth of approximately one foot. On arrival at the laboratory, they were immediately spread out in a thin layer and air dried. Each sample was thoroughly mixed and passed through a quarter-inch sieve to remove the stones and larger roots.

Terra cotta pots of six-inch diameter, coated with a double layer of black bituminous paint and with small watch glasses as crocks, were filled with 1400 g. of air-dry soil. Nutrients are liberated from plastic pots, which are therefore unsuitable for this work.

Distilled water or nutrient solution was added to saturate the soil. Each pot was placed on a glass saucer so that any drainage water could be collected and recirculated through the soil to avoid loss of nutrients.

Well-developed seedlings of comparable vigour, which had been raised on wet filter paper, were planted and supplied with distilled water as required. The pots were placed at random in a long narrow strip against a north-west facing glasshouse wall, so that all would receive equal illumination and temperature.

The growth of the shoot systems of the individual plants within each pot was relatively even, particularly in the case of horticultural species, and in these instances each pot was treated as a single unit at harvesting, individual plants being bulked. The shoot systems were dried at 60°C. and weighed.

Details of Nutrient Treatments.

For "+ P" treatment, NaH_2PO_4 was added.

For "+ N" treatment, $NaNO_3$ was added.

For "+ Ca" treatment, $CaCl_2$ was added.

"Complete–N" solution. 2·5 ml. M KH_2PO_4, + 0·4 ml. M $CaCl_2$ + 100 ml. water were mixed with each 1400 g. soil which had been spread out on waterproofed paper. The soil was returned to the pot and 380 ml. of the following solution added.

Solution "A". 2 ml. M $MgSO_4$ + 1 ml. trace element solution + 1 ml. 0·5% ferric tartrate + 1900 ml. water.

"Complete–P" solution. 50 ml. M KNO_3 + 2 ml. M $CaCl_2$ were added into solution "A". 380 ml. of this solution per 1400 g. of soil were used.

"Complete" solution. 2·5 ml. M KH_2PO_4 + 100 ml. water were added to each 1400 g. soil. 2 ml. M $CaCl_2$ + 25 ml. M KNO_3 were added into solution "A". 380 ml. of this solution were added to each pot.

Trace Element solution. The trace element solution had the following composition and was used at the rate of 1 ml./litre of nutrient solution:

Element and Reagent.	Concentration of Reagent in Trace Element Solution. (g./l.)	Final Concentration of Element in Nutrient Solution. (p.p.m.)
Boron as H_3BO_3	2·86	0·5
Manganese as $MnSO_4.4H_2O$	2·04	0·5
Zinc as $ZnSO_4.7H_2O$	0·22	0·05
Copper as $CuSO_4.5H_2O$	0·08	0·02
Molybdenum as $H_2MoO_4.H_2O$ (assaying 85% MoO_3)	0·02	0·01

The selection of a species to serve as an indicator of the nutrient status of the soils was difficult. A rapidly growing upright type, tolerant of acid conditions and with a long period of vegetative growth, was required. Radish (*Raphanus sativus* L.), turnip (*Brassica rapa* L.), *Spinacia oleracea* L., *Eupatorium* L., *Portulaca grandiflora* Hook., lettuce (*Lactuca sativa* L.), snapdragon (*Antirrhinum majus* L.), and *Euphorbia* L. failed to develop satisfactorily in these soils. Tomato (*Lycopersicon esculentum* Mill.) and flax (*Linum usitatissimum* L.) grew only moderately well in the forest soils; however, tomato failed to survive in swamp soils and the flax developed a fasciated or bifurcated stem condition mentioned by Kerr (1953). However, barley (*Hordeum vulgare* L.), oats (*Avena sativa* L.) and particularly rice (*Oryza sativa* L.) were found to grow satisfactorily in these conditions.

Results and Discussion.

Table 1 shows values for the dry weight of the shoots of rice which were grown under various nutrient treatments. Only a single mean value for the growth in eucalypt forest and shrub swamp soils is given, since the locality-treatment interaction term is not significant ($F = 0{\cdot}99$). The treatment term is highly significant ($P < 1\%$).

TABLE 1.

Dry Weight of Rice (Oryza sativa *L.*) *Shoots under Various Nutrient Treatments.*

Plants grown in Hawkesbury Sandstone soils for eight weeks, water being maintained at field capacity.

Nutrient Treatment.*	Nutrient Concentration (p.p.m.).	Mean Weight per Pot of Four Plants in Eucalypt Forest or Shrub Swamp Soil (mg.).	Treatment Number.	Significance.	
				$P=0{\cdot}05$.	$P=0{\cdot}01$.
Complete ..	—	2753	1	>2–12	>2–12
$+P_2O_5+N$ ..	+125+50	2550	2	>3–12	>3–12
$+P_2O_5+N+Ca$	+125+50+11	1861	3	>4–12	>4–12
$+P_2O_5$ ..	75	1689	4	>5–12	>5–12
Complete −N ..	—	1339	5	>6–12	>6–12
$+P_2O_5$ ..	125	1080	6	>7–12	>7–12
$+P_2O_5$ ..	5	688	7	>8–12	>7–12
+N	30	556	8	—	—
+N	50	496	9	—	—
+N	2	472	10	—	—
Water	—	469	11	—	—
Complete −P ..	—	449	12	—	—

Weight of plants grown in washed river sand = 176 ± 24 mg. This represents growth due to seed reserves.

The difference necessary for significance : $P=0{\cdot}05$: 89 mg. ; $P=0{\cdot}01$: 120 mg.

* Details of the nutrient treatments are given on page 122.

The increased growth of plant shoots in the presence of phosphate as compared with the controls and the close agreement between (i) "complete–P", "+N" and control treatments and (ii) "+P+N" and "complete" treatments, demonstrate very clearly the lack of phosphorus in the soils and the overriding significance of the deficiency of phosphorus and nitrogen as compared with other nutrients.

"Complete–N" compared with "complete" growth reflects the low level of nitrogen, and the poor growth in "+N" shows its place as secondary to that of phosphorus in the nutrient status of these soils.

Depression of growth with "+125 p.p.m. P_2O_5" as compared with 75 p.p.m. may be due to a lack of balance of nutrients, owing to the addition of a single salt. A depressing effect of high or moderately high levels of phosphorus on plant growth has been recorded by a number of workers (Rossiter, 1952). This effect is more marked in conditions of low nitrogen supply.

The less vigorous growth occurring in "+P+N+Ca" as compared with "+P+N" is surprising, since chemical analyses of the soils show very low levels of calcium (Storrier, 1951).

It is of interest to note that the only instance where the addition of nitrogen, in the presence of phosphorus, did not prove a stimulus to growth is in *Acacia suaveolens* (Sm.) Willd., a typical and commonly nodulated member of the dry sclerophyll scrub communities (Table 2). It is found only occasionally in swamps and then towards the edge of the communities. Growth was more vigorous where nutrients were added in the forest than in the swamp soil. The locality-treatment interaction term is highly significant ($F = 30{\cdot}58$; $F_{P=0{\cdot}01} = 6{\cdot}93$); therefore the results have been presented for both the forest and swamp soils. The treatment and locality terms are both very significant ($P < 0{\cdot}01$). The root systems were nodulated in all treatments, but apparently not very effectively in the swamp soil and most effectively in the forest soil with added phosphate.

Casuarina littoralis Salisb. is a prominent member of the dry sclerophyll scrub and forests and is often nodulated in the field. Analysis of the experimental results shows that the locality-treatment interaction term is significant at the 5% level. A comparison of the growth made in the two soils shows that the only significant difference between soils occurs in "+ P + N" treatment. *Casuarina* did not respond so markedly to the addition of nitrogen in the swamp soil. The explanation for this result is not clear. No nodules were found on the root systems in any of the treatments. It can only be said that *Casuarina* is not found growing in swamp communities under natural conditions, and apparently its development is hampered by some character of the swamp soils.

No interaction between treatment and locality is in evidence in either *Eucalyptus gummifera* (Gaertn.) Hochr. ($F = 1{\cdot}96$; $F_{P=0{\cdot}05} = 3{\cdot}88$) or *Hakea dactyloides* (Gaertn.) Cav. ($F = 1{\cdot}07$; $F_{P=0{\cdot}05} = 3{\cdot}88$). In both species the treatment term is highly significant ($P < 0{\cdot}01$). *E. gummifera* is a very widespread member of most communities and very often is found fringing swamp communities. *H. dactyloides* is one of the Proteaceae. This is one of the most common families of the native flora and its members dominate dry and swamp scrub.

Photographs of each of these species growing under the various treatments are shown in Plate x.

Level of Nitrogen in Hawkesbury Sandstone Communities.

Tables 3–18 are presented to show the range of nitrogen found in the parent material, soils and vegetation in Hawkesbury Sandstone communities.

Method.

There is a tremendous amount of literature on the use of the Kjeldahl method for nitrogen determinations. The position is perhaps best summarized by Kirk (1950): "The present status of the Kjeldahl method leaves much to be desired in spite of its wide use."

The choice of the catalyst appears to be the most important factor in the determination of nitrogen, especially with respect to the rate and efficiency of the conversion of the nitrogenous compounds to ammonium sulphate. Cupric sulphate, mercuric oxide and elemental selenium appear to be the most commonly used.

In the present investigation, total nitrogen analyses were made using the Kjeldahl method in main essentials as outlined by Jensen (1940). Nitrate is reduced with zinc powder and then potassium sulphate and copper sulphate are added. Selenium gave lower nitrogen values in soil analyses, and sometimes disagreement between replicates was noted where mercury was included in the digestion mixture, even though sodium thiosulphate was added at the time of distillation. Duplicate digestions were made of each sample and only figures showing no greater difference than 2% were accepted; most analyses differed by no more than 1%.

Parent Material.

Results and Discussion.

The incidence of fossils in Hawkesbury Sandstone is very low, but apparently this series was laid down under water containing nitrogen (Table 3). The nitrogen level

TABLE 2.

Dry Weight of Shoots of Native Species under Various Nutrient Treatments.

Plants grown in Hawkesbury Sandstone soils for eight months, water being maintained at field capacity.

Acacia suaveolens (Sm.) Willd.

Soil.	Nutrient Treatment.	Mean Weight per Pot of Three Plants. (g.).	Treatment Number.	Significance.	
				P=0·02.	P=0·01.
Eucalypt forest soil.	+P+N*	15·07	1	—	>3
	+P	17·87	2	>1–3	>3
	+Water	3·33	3	—	—
Shrub swamp soil.	+P+N	11·13	1	—	>2–3
	+P	6·07	2	—	>3
	+Water	2·33	3	—	—

The difference necessary for significance: P=0·02 : 2·709 g.; P=0·01 : 3·092 g.

Casuarina littoralis Salisb.

Soil.	Nutrient Treatment.	Mean Weight per Pot of Three Plants (g.).	Treatment Number.	Significance.	
				P=0·02.	P=0·01.
Eucalypt forest soil.	+P+N	9·03	1	—	>2–3
	+P	4·40	2	—	>3
	+Water	1·90	3	—	—
Shrub swamp soil.	+P+N	6·33	1	>2–3	>3
	+P	4·20	2	>3	—
	+Water	2·23	3	—	—

The difference necessary for significance: P=0·02 : 1·930 g.; P=0·01 : 2·203 g.

Eucalyptus gummifera (Gaertn.) Hochr.

Nutrient Treatment.	Mean Weight per Pot of Three Plants in Eucalypt Forest or Shrub Swamp Soil (g.).	Treatment Number.	Significance P=0·01.
+P+N	9·87	1	>2–3
+P	5·19	2	>3
+Water	2·07	3	—

The difference necessary for significance: P=0·01 : 0·707 g.

Hakea dactyloides (Gaertn.) Cav.

Nutrient Treatment.	Mean Weight per Pot of Three Plants in Eucalypt Forest or Shrub Swamp Soil (g.).	Treatment Number.	Significance P=0·01.
+P+N	16·25	1	>2–3
+P	10·30	2	>3
+Water	5·40	3	—

The difference necessary for significance: P=0·01 : 1·415 g.

* The concentration of added nutrients throughout Table 2 is as follows: $+P_2O_5$: 125 p.p.m.; +N: 50 p.p.m.

of rocks is rarely reported. Hall and Miller (1908) give values ranging from 40 to 90 p.p.m. nitrogen for sandy rocks and 330 to 1070 p.p.m. for shales. Urey (1953) quotes Hutchinson's value of 510 p.p.m. nitrogen in sedimentary rocks, but notes that the shales and red clay of the sea bottom have been weighted most heavily in estimating an average value for sedimentary rocks.

The nitrogen content of the Hawkesbury Sandstone rock is a significant fraction of that found in the soils (Table 3), but in each instance it is obvious that nitrogen accretion has occurred with the development of soil and plant communities.

TABLE 3.

Total Nitrogen Content of Unweathered Hawkesbury Sandstone and Surface Soil (0–8 in.) Samples.

Site.	Total Nitrogen (on Oven Dry Basis)* (p.p.m.).	
	Rock.	Soil.
Darke's Forest Road	170	620
National Park	210	290
Pearl Beach	160	640
French's Forest	150	330
Kuring-gai Chase	200	350

* In all subsequent tables, nitrogen values are expressed on an oven dry basis.

SOILS.

The soils are immature sandy iron podsols and, like European podsols, have a low base saturation and an acid reaction. They lack the high exchange capacity of the surface horizon of the European podsols (Storrier, 1951).

(i) Total Nitrogen.

Method.

At each site, aerial growth was removed and large samples (at least 10 kg.) of soil were collected. Except for the profiles, for which depths of sampling are indicated in Table 8, surface samples to a depth of approximately eight inches were taken. Prior to chemical analysis the soils were passed through a 2-mm. sieve and then thoroughly mixed. Subsamples were taken by coning and quartering until a sample of several hundred grammes remained. It was considered that any root pieces which passed through the sieve belonged, at least potentially, to the soil organic matter fraction. Special precautions were taken to ensure that root pieces were thoroughly mixed throughout the sample, as they separate readily from the coarser grained soil particles. Where necessary, the sample was ground more finely to pass a 0·5-mm. sieve; all samples for organic carbon analysis were ground to this state.

The nitrogen content of the soils has been expressed as a concentration, on a dry weight basis, since this is the usually accepted procedure. Expression on an absolute basis, taking an account of soil volume, probably has more meaning; but since the sandstone samples are similar throughout in structure and density, direct comparison of concentration values should be quite satisfactory.

Results.

The mean values of the nitrogen content of the soils in Table 4 are each based on the analysis of several samples collected within each of the formations at the given localities. For the present purpose the variability within the sites is considered to be of a sufficiently low order to justify the collection of single samples from each site.

Examination of Table 5 shows that, apart from the swamps, there is a general trend for higher formations to occur on soils with a higher nitrogen content. If the density and growth form of the vegetation be taken into consideration, the total nitrogen content expressed on an area basis for each community could be expected to show far greater differences.

TABLE 4.

Variability of Soil Nitrogen Content within Community Sites.

Formation.	Total Nitrogen (p.p.m.).
Low scrub forest at Jannali (8)	400±56
Wet sclerophyll forest at Pearl Beach (3)	920±70
Shrub swamp at Jannali (3)	1340±90
Shrub swamp at Loftus (3)	1530±72

The numbers in brackets refer to the number of samples analysed from each community.

In view of the results in Table 5, the figures of the valley sequence samples in Table 6 are much as would be expected, since plant growth in the valley at Warrah was much more luxuriant than that at Jannali.

TABLE 5.

Nitrogen Content of Soils from Typical Communities in Various Localities.

Formation.	Total Nitrogen (p.p.m.).
Scrub (2)	360± 90
Tree scrub (3)	410± 42
Low scrub forest (4)	300± 26
Tall scrub forest:	
Dry sclerophyll (4)	530±114
Dry-wet sclerophyll transition (3)	820±176
Wet sclerophyll (3)	1010±268
On shale lens (2)	1030± 85
Sedge swamp (5)	910±189
Shrub swamp (8)	1110±155

The numbers in brackets refer to the number of localities from which samples in each formation were taken.

In collecting the swamp samples mentioned in Table 5, central position in each swamp was chosen as sampling site (see Table 7).

The swamps are amongst the richest of the sandstone soils with regard to nitrogen content. Samples were collected along the slope of swamps, from near the outcropping rock ledge where water accumulation and algal growth are greatest, back through

TABLE 6.

Valley Sequence Samples.

Nitrogen Content of Soils at Various Depths.

Formation.	Total Nitrogen (p.p.m.).
Warrah Sanctuary:	
Wind swept scrub	700
Low scrub forest (immediately below scrub)	640
Low scrub forest	440
Tall scrub forest	830
In *Casuarina* stand	1030
Wet sclerophyll forest	980
Jannali:	
Open scrub	400
Low scrub forest	400
Tall scrub forest (dry sclerophyll)	470

increasing soil depth where surface soil water decreases. An average slope of swamps is approximately 1/12. It is seen that soil nitrogen is highest where water accumulation and algal growth are greatest (Table 7). The significance of this will be discussed in a later publication.

TABLE 7.

Shrub Swamp Transects.

Position of Sample in Swamp.	Total Nitrogen (p.p.m.).
Kuring-gai Chase :	
Close to rock edge : much algal growth	1960
Approximately 48 ft. above rock	1500
,, 96 ft. ,, ...	1300
,, 144 ft. ,, ...	1080
Close to fringing tree scrub	600
Waterfall :	
Close to rock edge	1120
Towards top edge of swamp	540
Jannali :	
At lower edge of swamp	1420
,, ,, ,, ,, ,, ...	1500
In middle of swamp	1060
At top edge of swamp	830
,, ,, ,, ,, ,, ...	660
,, ,, ,, ,, ,, ...	730
,, ,, ,, ,, ,, ...	660

While the nitrogen content of the soil decreases with depth throughout (Table 8), the sublayers of the swamp soils are relatively much richer than the dry sclerophyll communities.

TABLE 8.

Vertical Distribution of Soil Nitrogen.

Formation and Sample Depth.	Total Nitrogen (p.p.m.).
Jannali scrub :	
0″– 6″	550
10″–14″	300
27″–30″	250
Jannali tall scrub forest :	
0″– 8″	650
18″–24″	370
36″–40″	490
Kuring-gai tall scrub forest :	
0″– 4″	450
4″–14″	330
14″–26″	250
French's Forest tall scrub forest :	
0″– 4″	430
4″–10″	220
10″–18″	270
French's Forest shrub swamp :	
0″– 2″	1100
2″– 8″	1060
8″–20″	1000
Kuring-gai shrub swamp :	
0″– 2″	1170
2″– 8″	1040
8″–20″	880

Discussion.

According to Taylor (1950), "it may be said that all soil groups in Australia except the red loams and black earths respond strongly to phosphatic fertilizers, while nitrogen is either an essential or at least a limiting factor in virgin areas". Taylor quotes the typical range for podsols as 300–>2000 p.p.m. nitrogen, with the most frequent values being 400–600 p.p.m. and 1000–2000 p.p.m.

Under virgin conditions the organic matter and nitrogen content of a soil approach an equilibrium value, the magnitude of which depends primarily upon climate, vegetation, microflora, the topography and the parent material. The sclerophyllous vegetation, mineral-deficient parent material and low water-retaining capacity of the Hawkesbury Sandstone soils would not be expected to favour the development of high levels of nitrogen. The great importance of climatic factors in determining the soil-nitrogen level has been demonstrated by Jenny (1930) for grassland and timbered soils in U.S.A. For cultivated soils from originally timbered areas, Jenny found that temperature controlled the soil-nitrogen content, moisture having little influence over a range of 125–375 N.S. quotients (Niederschlag und Sättigungsdefizit—precipitation/saturation deficit values).

Prescott (1952) has stated that in Australia the effect of temperature is to reduce the efficiency of rainfall through its effect on evaporation and that no evidence of a direct effect on nitrogen content of the soil is to be observed, apart from its important effect on the rate of decomposition of organic matter as well as its production. However, for sake of comparison with Jenny's work on timbered soils, some of his figures are mentioned. In regions of annual temperature of 62°F., Jenny's value for soil nitrogen content is 570 ± 60 p.p.m., and for 64°F., 510 ± 30 p.p.m. Sydney's mean annual temperature is 63°F. and the N.S. quotient is 250.

Prescott suggests from the limited data available that in Australia the nitrogen content of soil is most closely related to the N.S. quotient. He also states that "A general examination of the records, together with a knowledge of general conditions in Australia, suggests a further important correlation between the nitrogen content of soil and the content of phosphoric acid". This certainly is of significance in Hawkesbury Sandstone soils in view of their great phosphate deficiency. Prescott reports that soils from Bundaberg, Queensland, of low phosphoric acid values show a high correlation with nitrogen content and those of high and very variable phosphoric acid values, no correlation, with a uniform nitrogen content independent of phosphate fluctuations.

In soils of the north-west wheatbelt of New South Wales, where total and available phosphorus is at a very high level, Hallsworth, Gibbons and Lemerle (1954) found no relationship between nitrogen and phosphorus in virgin soils.

It thus is obvious that the nitrogen content of these soils is low but comparable with similar types of soil in other areas. However, their high C/N ratios and low pH values tend to reduce the value of their nitrogen content as far as plant growth is concerned.

(ii) pH and Organic Carbon.

Apart from total nitrogen content of soils, other properties relevant to the availability of nitrogen for plant growth are pH values and the carbon-nitrogen ratio of the soils.

Method.

pH readings were made on a Jones Model B glass electrode potentiometer with sufficient water to give the equivalent of sticky point in the soil.

Table 9 shows that a distinctly acid reaction is common to all samples.

Organic carbon was determined by the Walkley-Black method, as outlined by Piper (1947). The results given in Table 10 are as carbon, and no correction has been made to account for incomplete recovery of the organic matter.

According to Walkley (1935), the Walkley-Black (1934) rapid method gives a mean recovery for most agricultural surface soils between 75 and 80%, taking dry combustion values as the standard of comparison. This method has the advantage of speed and

TABLE 9

pH Values of Surface (0–8 in.) Soil Samples.

Formation.	Location.	pH.
Scrub	Waterfall	4·8
Tree scrub	Loftus	5·0
	Jannali	4·6
Low scrub forest	Linden	3·8
	Helensburgh	4·7
	Waterfall	4·8
Tall scrub forest:		
Dry sclerophyll	East of Darke's Forest	4·4
	North of Bulli	4·7
	Waterfall	4·5
Dry-wet sclerophyll	Berowra	4·5
Sedge swamp	Waterfall	4·6
	Bulli	4·4
	South of Waterfall	4·7
Shrub swamp	Warrah Sanctuary	4·5
	Kuring-gai	4·8
	Waterfall	4·6
	Waterfall	4·7
	Jannali	4·7

TABLE 10.

Organic Carbon Content of Soils.

Formation and Location.	Total Nitrogen (p.p.m.).	Organic Carbon (p.p.m.).	C/N.
Scrub:			
South of Waterfall	450	12,000	26·7
Ocean Beach Dunes—*Leptospermum*	470	15,700	33·4
Tree scrub:			
Waterfall	410	10,500	25·6
Low scrub forest:			
Helensburgh	330	8,000	24·2
Ocean Beach Dunes—*Banksia*—*E. botryoides*	230	10,600	46·1
Ocean Beach Dunes—*Eucalyptus pilularis*	300	13,600	45·3
East of Darke's Forest	—	14,000	—
Tall scrub forest:			
Dry sclerophyll forest:			
East of Darke's Forest	620	22,400	36·1
Appin Road	400	15,500	38·7
National Park	290	7,000	24·1
Dry-wet transition:			
Berowra	470	13,000	27·7
Warrah Sanctuary	980	22,400	22·9
Warrah Sanctuary	1,000	22,900	22·9
Wet sclerophyll:			
Warrah Sanctuary	700	18,500	26·4
Berowra	1,540	28,000	18·2
Pennant Hills	780	17,200	22·1
On shale lens:			
Bulli	1,110	27,500	24·8
Pennant Hills	940	21,000	22·3
Sedge swamp:			
Madden's Plains	1,630	37,500	23·0
Loftus	670	10.600	15·8
Waterfall	900	24,200	26·9
Appin Road	750	18,600	24·8
Shrub swamp:			
Bulli	770	20.700	27·0
Waterfall	530	25,400	47·9
Jannali	1,050	52,100	49·6
Warrah Sanctuary	1,830	35,200	19·3

even relative figures are of considerable value for this purpose. Even though the carbon contents of the soils as given in Table 10 are high, it is seen that they are underestimated by the use of this method.

Results and Discussion.

As organic residues decompose, there is a narrowing of the C/N ratio until an equilibrium value of about 12 is reached. Russell (1950) has stated that "A C/N ratio of around 10 is very common for English arable soils". The wide ratios, as exist in the Hawkesbury Sandstone soils (Table 10), indicate that much of the organic matter is in only very early stages of decomposition, apparently blocked at this point by a limiting factor, resulting in the accumulation of an organic complex. The nature of this supposed limiting factor has not been investigated, but the character of the organic matter of soils is determined largely by the character of the vegetation. The low level of nitrogen in the highly lignified plant material (see Table 14) and in the soil probably is the cause of lack of formation of typical "humus". The general low level of other mineral elements, especially phosphorus, and the low pH values would militate against rapid decomposition of litter and hence lead to slow humus formation.

Experimental work on the nature of the organic matter in Hawkesbury Sandstone soils would be of considerable interest. Respiration studies by means of the Warburg technique (Rovira, 1953) to measure the carbon dioxide evolved and hence the microbial activity would give valuable data. Attempts to increase the rate of narrowing of the C/N ratio by addition of nitrogen and phosphorus should prove especially interesting.

Parberry and Swaby (1942) studied the release of nitrogen from different organic materials added to soils and found that sufficient nitrogen for crop needs was liberated in one season only from materials containing an initial nitrogen content of greater than 25,000 p.p.m. No nitrogen was liberated in this period from materials having less than 15,000 p.p.m. nitrogen. Waksman and Tenney (1927) state that 17,000 p.p.m. nitrogen in plant material is adequate for microbial needs. Bledsoe (1937) concluded that if the water-soluble nitrogen content is 5,000 p.p.m. or above, favourable nitrate accumulation occurs, even though the total nitrogen content is less than 17,000 p.p.m. The native vegetation shows no level of soluble nitrogen comparable with this figure or even total nitrogen exceeding 15,000 p.p.m. (Table 14).

Hosking (1935) has made an extensive investigation of the C/N ratio of Australian soils in nine zonal groups. His records show great variation in organic matter content, not only between different soil types, but also within each type. Using a dry combustion method, he found that C/N of podsol surface samples ranged from 10 to 33. Of 50 samples, 68% fell between 10 and 20, and of these, 54% between 14 and 20. Hosking's figures for surface podsol samples (0–9″) are shown in Table 11. For comparable soils in North America, Hosking quotes a mean value of 21·8 for C/N of Quebec Province and 16·3 for United States soils.

TABLE 11. (Taken from Hosking, 1935.)
Carbon and Nitrogen Contents of Australian Podsol Surface Samples.

Factor.	Minimum.	Maximum.	Mean.
C/N	10·0	32·9	19·1±0·8
P.p.m. Carbon	2,200	95,600	32,500
P.p.m. Nitrogen	190	5,400	1,730

Due to the much higher mean value of 1,730 p.p.m. nitrogen of Hoskings' samples in comparison with those of Hawkesbury Sandstone, the latter's C/N ratios are the higher, but even so they are likely to have been underestimated in comparison with Hoskings', since they have been determined by a wet combustion method.

(iii) Available Nitrogen.

The level of available nutrients in any soil at any particular time depends on the balance existing between the rate of their formation from the soil reserve and the rate of their removal by growing plants, the soil population and leaching. In any ecosystem, available nutrients present in the soil represent at least a temporary excess over the requirements of the various members. Such an excess of nitrogen is unlikely to occur in a mineral-deficient soil of such a high carbon-nitrogen ratio as that derived from Hawkesbury Sandstone, since the phosphorus level would probably limit the activity of the microbial population just as it does plant growth.

Therefore, only few chemical analyses of available nitrogen in soil have been made. It is felt that a measure of the rate of production of available nitrogen from the soil organic reserve is a better indication of the nitrogen-supplying power of a soil than the absolute amount of available nitrogen present in the soil at any given time. This is especially pertinent in soil where the rate of decomposition of organic matter is low and the naturally occurring plants are slow-growing perennials.

Method.

(a) Chemical Analysis.

Soil extracts were prepared following Piper's method (1951, unpublished data), in which a solution of pH 1·8 of sodium sulphate and copper sulphate in concentrated sulphuric acid is used for the extraction. Ammonia was estimated colorimetrically with Nessler reagent and the nitrate nitrogen by the xylenol method (Piper and Lewis, 1951, unpublished data).

Results.

Nitrate nitrogen was detected in several soil samples on one occasion, and the highest value was 2 p.p.m. in the surface layer of a swamp (0–4″). During a period of hot weather following good rains, no nitrate was found in any of 18 samples. The soils are very light in texture and their nitrate content would be markedly affected by leaching.

Ammoniacal nitrogen was consistently present and values of 1–2 p.p.m. nitrogen were usual.

These values are much lower than those given by Beadle and Tchan (1955*a*) for soils in western New South Wales where nitrogen is limiting plant growth. Total available nitrogen in these soils averages 12 p.p.m.

Russell (1950) gives the following figures for the mineral nitrogen content of the surface layers of cultivated soils. Grassland: approx. 5 p.p.m. as ammonium and 1·2 p.p.m. as nitrate. Arable soils of moderate pH: "a constant but low content of ammonium nitrogen but a very variable nitrate content ranging from 2–20 p.p.m.". A rich garden soil may contain up to 60 p.p.m. nitrate nitrogen.

Süchting (1949) has recorded that of the total nitrogen present in forest soils, 90–95% is unavailable as heterocyclic polyoxy compounds of high molecular weight, the lignin-protein complexes.

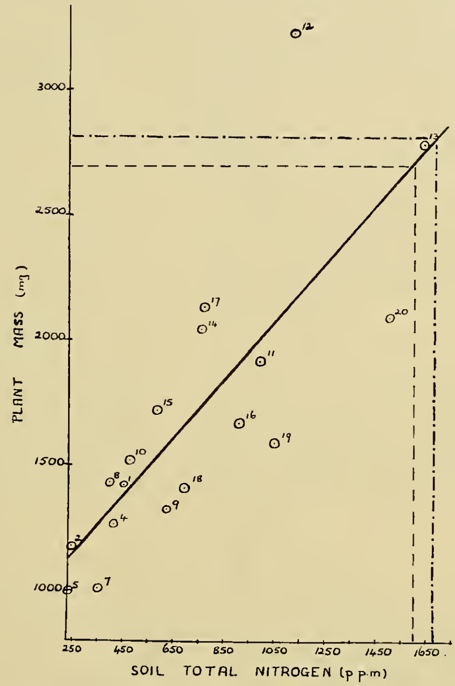
(b) Bioassay.

Incubation of soil with chemical analysis of samples taken at frequent intervals would allow a thorough study of the mineralization of soil organic matter. However, a bioassay experiment has provided some information. A bioassay lacks the precision of the more thorough study in that only a single final value is obtained and a greater number of sources of error is involved.

Details of the preparation of soils and pots were the same as described for the other glasshouse experiments. Since phosphorus is the prime limiting factor in the soils and plant growth would be hindered in its absence, a mineral solution complete but for nitrogen was added to the soils. Thus the soil's reserve of nitrogen would be the only source available for plant growth. The addition of nutrients would probably cause increased nitrification of the organic matter, but it appears that this disadvantage cannot be avoided. The results are given in Table 12 and Text-figure 1.

Results and Discussion.

Analysis of the plant yields listed in Table 12 shows that the locality term is highly significant ($F = 18{\cdot}33$; $F_{P=0{\cdot}01} = 2{\cdot}97$). The regression line to the points in Text-figure 1 has been fitted. Analysis of this straight line equation shows that there are significant deviations of some points from this line, but it is obvious that the fitting of a quadratic equation would be no improvement. Nevertheless the regression coefficient is very significant ($F = 7{\cdot}26$; $F_{P=0{\cdot}05} = 4{\cdot}49$; $F_{P=0{\cdot}01} = 8{\cdot}53$).



Text-fig. 1.—Relationship between the growth of rice and soil total nitrogen. ⊙: mean weight per pot of four plants in each of the soils. Numbers refer to the yield numbers in Table 12. ———: regression line fitted to points ⊙. $Y = 862{\cdot}4 + 1{\cdot}16x$. - - - -: Waterfall tree scrub soil + 50 p.p.m. nitrate-nitrogen. -·-·-·: Kuring-gai shrub swamp soil + 50 p.p.m. nitrate-nitrogen

With the exception of numbers 3 (a tree scrub occurring on a shale lens) and 18 (a swamp with a lower than average nitrogen content) it is seen from Table 12 that the plant yields fall into two classes which correspond with the following grouping of formations:

a. Scrub, tree scrub, low scrub forest and dry sclerophyll forest.

b. Dry-wet sclerophyll transition, shale lens samples and swamps.

Thus more vigorous plant growth developed where soil total nitrogen is high. More nitrogen is available for plant growth in the higher formations and swamps, i.e., the available nitrogen is proportional to the total nitrogen in these soils. This is as expected, since the nature and nitrogen content of the readily oxidizable fraction of the organic matter would be much the same throughout all communities—the chief difference between formations would be in the amount of organic matter present (Table 10).

Nitrate nitrogen was added to two of the soils as an additional treatment, so that an indication of the absolute level of available nitrogen liberated from the organic matter might be given. These results are shown in Table 13.

TABLE 12.

Dry Weight of Rice Shoots in Various Soils.

Plants were supplied with "Complete-N" mineral solution and water to field capacity for eight weeks.

Formation.	Locality.*	Soil Total Nitrogen (p.p.m.).	Plant Yield.† (mg.).	Yield Number.	Significance.‡
Scrub	S. of W.	450	1419	1	2, 4, 5, 7, (9).
	O.B.D.	240	1177	2	5, 7.
Tree scrub	D.F.R.§	—	1992	3	1, 2, 4, 5, 6, 7, 8, 9, 10, 15, 16, 18, 19.
	W.	410	1267	4	(2), 5, 7.
Low scrub forest ..	O.B.D.	230	1002	5	
	D.F.R.	—	1533	6	(1)¶, 2, 4, 5, 7, (8), 9, 18.
	L.	350	1006	7	
Tall scrub forest:					
Dry sclerophyll ..	A.R.	400	1432	8	2, 4, 5, 7, (9).
	E.D.F.	620	1320	9	2, 5, 7.
Dry-wet sclerophyll transition ..	B.	470	1519	10	(1), 2, 4, 5, 6, 7, (8), 9, (18).
	W.S.	980	1909	11	1, 2, 4, 5, 6, 7, 8, 9, 10, 15, 16, 18, 19.
	Bl.§	1110	3231	12	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20.
Sedge swamp	M.P.	1630	2780	13	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 13, 14, 15, 16, 18, 19, 20.
	A.R.	750	2046	14	1, 2, 4, 5, 6, 7, 8, 9, 10, 11, 15, 16, 18, 19.
	Bl.	580	1715	15	1, 2, 4, 5, 6, 7, 8, 9, 10, 18, 19.
	W.	900	1663	16	1, 2, 4, 5, 6, 7, 8, 9, 10, 18.
Shrub swamp ..	Bl.	770	2127	17	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 15, 16, 18, 19.
	K.	690	1410	18	2, 4, 5, 7, (9).
	J.	1050	1589	19	1, 2, 4, 5, 7, 8, 9, 18.
	W.	1500	2091	20	1, 2, (3), 4, 5, 6, 7, 8, 9, 10, 11, 15, 16, 18, 19.

Growth due to seed reserves in washed river sand = 176 ± 24 mg.

The differences necessary for significance: P = 0·05: 86 mg.; P = 0·02: 105 mg.; P = 0·01: 118 mg.

* Locality abbreviations: S. of W. = South of Waterfall; O.B.D. = Ocean Beach Dunes; D.F.R. = Darke's Forest Road; W. = Waterfall; L. = Linden; A.R. = Appin Road; E.D.F. = East of Darke's Forest; B. = Berowra; W.S. = Warrah Sanctuary; Bl. = Bulli; M.P. = Madden's Plains; K. = Kuring-gai; J. = Jannali.

† "Yield" represents the mean weight per pot of four plants.

‡ This column gives the numbers of the yields which are significantly less than the yield in question. (P = 0·01, except those marked ( ) ¶, when P = 0·02 and ( ) when P = 0·05).

§ Soil sample collected from a shale lens in the sandstone.

TABLE 13.

Dry Weight of Rice Shoots under Various Nutrient Treatments.

Plants were grown in soil for eight weeks, water being maintained at field capacity.

Nutrient Treatment.	Yield (mg.).	
	Waterfall Tree Scrub.	Kuring-gai Shrub Swamp.
Complete	2701	2805
Complete −N	1267	1410
+ Water	470	467

The difference necessary for significance: P = 0·01: 186 mg.

* The concentration of the added nutrients is as follows: $+P_2O_5$: 125 p.p.m.; +N: 50 p.p.m.

From Text-figure 1 it is seen that where 50 p.p.m. of available nitrogen was added to the Waterfall tree scrub soil, plant growth equivalent to a 1600 p.p.m. level of total nitrogen was produced. Thus 50 p.p.m. of available nitrogen is equivalent to 1190 p.p.m. total nitrogen, since the total nitrogen value for this soil is only 410 p.p.m. (Table 12). It follows that over a period of eight weeks only $\frac{50}{1190} \times 410 = 17{\cdot}2$ p.p.m. nitrogen became available from the soil organic matter. This is under conditions of water and all nutrients other than nitrogen being in full supply; under field conditions this value would be markedly reduced. Glasshouse temperature ranged from 17°C. to 33°C. during this period. Even this value of 17 p.p.m. would be an over-estimate, since micro-organisms are better able to compete for the added nutrients than the growing plant (Russell, 1950). It is therefore to be expected that only part of the added 50 p.p.m. nitrogen would have been taken up by the plant.

In the Kuring-gai shrub swamp soil, which has a higher total nitrogen content than the Waterfall sample, 34·8 p.p.m. nitrogen became available under the same conditions. From the data in Table 12 it appears that in the selection of a swamp sample the choice of the Kuring-gai swamp was somewhat unfortunate. Chemical analyses which were made later showed that it had a nitrogen content which is below average for swamps. Nevertheless, even in this sample twice the amount of nitrogen became available as did in the tree scrub soil. Under field conditions nitrate production may be hampered in swamps due to restricted aeration.

Harmsen and Lindenbergh (1949) describe a soil, which in successive weeks produced 7, 9, 10, 10, 10, 9 p.p.m. available nitrogen, as one with a very poor nitrogen nutrition for plants. A rich nitrogen nutrition for plants is ensured in a soil producing 27, 46, 60, 65, 68, 69, 68 p.p.m. available nitrogen in successive weeks. In both instances these soils were incubated in darkness in a saturated atmosphere at 29°C. with a moisture content of 60–70% of the total moisture-holding capacity.

PLANT MATERIAL.

(i) Leaf Analyses.

Method.

Only healthy mature leaves were collected for chemical analysis. The samples were taken from several positions on each plant, bulked, and subsamples were chosen for analysis. As far as possible, sampling from the various localities for each species was done in the same month to avoid any seasonal variation. However, from the results of Mitchell (1936) and Tamm (1951), who studied the nutrient composition of leaves of different ages in deciduous species, it would appear unlikely that the leaf nitrogen content would vary with season in the mature samples that were selected, since the species occurring in Hawkesbury Sandstone communities have long-lived evergreen foliage.

Results and Discussion.

The consistently higher value of legume leaf tissue as compared with non-leguminous material (Table 14) is of interest, and probably is linked with the presence of nodules capable of nitrogen fixation on their root systems. The few legume species that have been tested are capable of nitrogen fixation when inoculated with appropriate rhizobia (Hannon, 1949). The Casuarinaceae also approach the value of the legumes, and nodules from which bacteria were isolated have been found on *Casuarina littoralis* and *C. torulosa* in the field. Their ability to fix nitrogen has not yet been tested, but Mowry (1933) has reported nitrogen fixation for nine other species of *Casuarina*. In the glasshouse experiment (Table 3) it was apparent that *C. littoralis*, unlike *Acacia suaveolens*, responded to the addition of nitrate. However, careful examination of the root systems of *Casuarina* showed that no nodules had developed, whereas they were very obvious in *Acacia*. Further investigations on this aspect of *Casuarina* in Hawkesbury Sandstone communities will be reported later.

Only few organic carbon values for leaf material are available; of these, all fall within the range of 35–40% on a dry-weight basis. Fraser (1948) records 45% organic carbon in *Casuarina* cladodes. The amount of lignification in the tissue will obviously influence the percentage nitrogen values. The aerial tissue of *Bossiaea scolopendria* is of cladode form and is very lignified. Cladodes are also present in *Casuarina*; *C. distyla* is a much more lignified species than either *C. littoralis* or *C. torulosa*. This accounts

TABLE 14.

The Concentration of Nitrogen in Mature Leaf Tissue.*

Species.	P.p.m. Total Nitrogen (on Dry Weight Basis).				
	Scrub.	Swamp.	Low Scrub Forest.	Tall Scrub Forest.	
				Dry-wet.	Wet.
Proteaceae :					
Banksia serrata L.f.	—	—	[1] 4,300	—	—
Banksia serrata	—	—	[2] 5,100	[3] 4,800	—
Banksia robur Cav.	—	[1] 4,300	[2] 4,400	—	—
Grevillea punicea R.Br.	—	[1] 5,100	[2] 7,500	—	—
Isopogon anethifolius (Salisb.) Knight	—	[1] 4,000	[2] 5,800	—	—
Persoonia lanceolata Andr.	—	[1] 6,700	[2] 5,000	—	—
Persoonia levis (Cav.) Domin	—	—	[1] 6,900	[2] 7,700	[3] 5,300
Persoonia levis	—	—	[4] 8,500	—	—
Persoonia levis	—	—	[5] 8,000	—	—
Petrophile fucifolia (Salisb.) Knight	—	[1] 5,500	[2] 5,800	—	—
Rutaceae :					
Eriostemon lanceolatus Gaertn. f.	—	—	[1] 8,000	—	—
Eriostemon crowei F. Muell.	—	—	[1] 7,600	[2] 8,700	—
Myrtaceae :					
Angophora costata (Gaertn.) J. Britt.	—	—	—	[1] 6,300	—
Angophora costata	—	—	—	[2] 7,500	—
Baeckea diosmifolia Rudge	—	[1] 7,200	—	—	—
Calytrix tetragona Labill.	—	[1] 6,700	—	—	—
Darwinia fascicularis Rudge	—	[1] 6,800	—	—	—
Eucalyptus gummifera (Gaertn.) Hochr.	—	[1] 9,000	[2] 6,200	[3] 9,000	—
Eucalyptus haemastoma Sm.	—	[1] 6,700	[2] 5,700	—	—
Eucalyptus pilularis Sm.	—	—	[1] 9,200	[2] 8,700	[3] 8,900
Eucalyptus pilularis	—	—	—	[4] 9,600	—
Leptospermum squarrosum Gaertn.	—	[1] 7,400	—	—	—
Leptospermum attenuatum Sm.	[1] 7,400	—	—	—	—
Leguminosae :					
Acacia discolor (Andr.) Willd.	—	—	[1] 12,600	[2] 16,500	—
Acacia suaveolens (Sm.) Willd.†	—	[1] 20,700	[2] 15,300	[3] 19,200	[4] 18,400
Acacia suaveolens	—	—	[5] 18,600	—	—
Bossiaea scolopendria Sm.†	—	—	[1] 8,800	—	—
Dillwynia ericifolia Sm.	—	—	[1] 11,000	—	—
Dillwynia floribunda Sm.	—	[1] 8,900	—	—	—
Gompholobium grandiflorum Sm.	—	—	[1] 10,900	—	—
Gompholobium latifolium Sm.	—	—	[1] 20,500	[2] 22,500	—
Pultenaea elliptica Sm.	—	[1] 12,300	[2] 10,000	—	—
Casuarinaceae* :					
Casuarina distyla Vent.	—	—	[1] 7,200	—	—
Casuarina littoralis Salisb.	[1] 13,100	—	[2] 10,000	—	—
Casuarina littoralis	—	—	[3] 12,900	—	—
Casuarina torulosa Ait.	—	—	—	[1] 11,700	[2] 11,500
Epacridaceae :					
Epacris microphylla R.Br.	—	[1] 5,700	—	—	—
Epacris pulchella Cav.	—	—	[1] 5,100	—	—
Monotoca elliptica (Sm.) R.Br.	[1] 9,300	—	[2] 9,500	[3] 7,500	—

* In species marked †, phyllodes or cladodes replace leaves.

For explanation of the small figures prefixing the nitrogen concentrations, refer to the footnote to Table 14.

FOOTNOTE TO TABLE 14.

Details of Leaf Samples.

Species.	Number in Table 14.	Locality ‡	Dominant Species in Community.	Month of Sampling.
Banksia serrata	1	N.P.	*Eucalyptus haemastoma-E. gummifera.*	July.
	2	O.B.D.	*Eucalyptus botryoides* Sm.-*Banksia serrata.*	March.
	3	W.S.	*Eucalyptus piperita* Sm. - *Angophora costata-Syncarpia glomulifera* (Sm.) Niedenzu.	March.
Banksia robur	1	W.S.	*Hakea teretifolia.*	January.
	2	W.S.	*Eucalyptus punctata* D.C.-*E. haemastoma.*	July.
Grevillea punicea ..	1	W.S.	*Hakea teretifolia.*	July.
	2	W.S.	*Eucalyptus punctata-E. haemastoma-E. gummifera.*	July.
Isopogon anethifolius ..	1	W.S.	*Hakea teretifolia.*	July.
	2	W.S.	*Eucalyptus punctata-E. haemastoma-E. gummifera.*	July.
Persoonia lanceolata ..	1	W.S.	*Hakea teretifolia.*	January.
	2	W.S.	*Eucalyptus punctata-E. haemastoma-E. gummifera.*	July.
Persoonia levis	1	N.P.	*Eucalyptus haemastoma-E. gummifera.*	July.
	2	W.S.	*Eucalyptus piperita-Angophora costata-Syncarpia glomulifera.*	March.
	3	W.S.	*Eucalyptus piperita-Angophora costata-Ceratopetalum apetalum* D. Don.	March.
	4	O.B.D.	*Eucalyptus botryoides-Banksia serrata.*	March.
	5	O.B.D.	*Eucalyptus pilularis.*	March
Petrophile fucifolia ..	1	W.S.	*Hakea teretifolia.*	January.
	2	W.S.	*Eucalyptus punctata-E. haemastoma-E. gummifera.*	January.
Eriostemon lanceolatus	1	N.P.	*Eucalyptus haemastoma-E. gummifera.*	July.
Eriostemon crowei ..	1	W.S.	*Eucalyptus punctata-E. haemastoma-E. gummifera.*	March.
	2	W.S.	*Eucalyptus piperita-Angophora costata.*	March.
Angophora costata ..	1	N.P.	*Eucalyptus piperita-Angophora costata.*	July.
	2	Bl.	*Eucalyptus piperita-Angophora costata.*	November.
Baeckea diosmifolia ..	1	W.S.	*Hakea teretifolia.*	March.
Calytrix tetragona ..	1	W.S.	*Hakea teretifolia.*	January.
Darwinia fascicularis	1	W.S.	*Hakea teretifolia.*	July.
Eucalyptus gummifera	1	W.S.	*Hakea teretifolia.*	January.
	2	W.S.	*Eucalyptus punctata-E. haemastoma-E. gummifera.*	January.
	3	W.S.	*Eucalyptus piperita-Angophora costata.*	March.
Eucalyptus haemastoma	1	W.S.	*Hakea teretifolia.*	March.
	2	W.S.	*Eucalyptus punctata-E. haemastoma-E. gummifera.*	January.
Eucalyptus pilularis ..	1	O.B.D.	*Eucalyptus pilularis.*	March.
	2	K.C.	*Eucalyptus pilularis-Angophora costata.*	March.
	3	P.H.	*Eucalyptus pilularis-Angophora costata.*	May.
	4	W.S.	*Eucalyptus piperita-Angophora costata.*	March.

FOOTNOTE TO TABLE. 14—*Continued.*

Details of Leaf Samples.—Continued.

Species.	Number in Table 14.	Locality.‡	Dominant Species in Community.	Month of Sampling.
Leptospermum squarrosum	1	W.S.	*Hakea teretifolia.*	July.
Leptospermum attenuatum	1	O.B.D.	*Leptospermum attenuatum.*	January.
Acacia discolor ..	1	N.P.	*Eucalyptus haemastoma-E. gummifera.*	July.
	2	W.S.	*Eucalyptus piperita-Angophora costata.*	March.
Acacia suaveolens ..	1	W.S.	*Hakea teretifolia.*	January.
	2	N.P.	*Eucalyptus haemastoma-E. gummifera.*	July.
	3	K.C.	*Eucalyptus pilularis-Angophora costata.*	March.
	4	W.S.	*Eucalyptus piperita-Angophora costata-Ceratopetalum apetalum.*	March.
	5	O.B.D.	*Eucalyptus botryoides-Banksia serrata.*	March.
Bossiaea scolopendria ..	1	W.S.	*Eucalyptus punctata-E. haemastoma-E. gummifera.*	January.
Dillwynia ericifolia ..	1	W.S.	*Eucalyptus punctata-E. haemastoma-E. gummifera.*	January.
Dillwynia floribunda ..	1	W.S.	*Hakea teretifolia.*	January.
Gompholobium grandiflorum.	1	W.S.	*Eucalyptus punctata-E. haemastoma-E. gummifera.*	January.
Gompholobium latifolium	1	O.B.D.	*Eucalyptus botryoides-Banksia serrata.*	March.
	2	W.S.	*Eucalyptus piperita-Angophora costata-Syncarpia glomulifera.*	March.
Pultenaea elliptica ..	1	W.S.	*Hakea teretifolia.*	January.
	2	W.S.	*Eucalyptus punctata-E. haemastoma-E. gummifera.*	January.
Casuarina distyla ..	1	W.S.	*Eucalyptus punctata-E. haemastoma-E. gummifera.*	January.
Casuarina littoralis ..	1	J.	Proteaceae spp.	March.
	2	O.B.D.	*Eucalyptus pilularis.*	March.
	3	O.B.D.	*Eucalyptus botryoides.*	March
Casuarina torulosa ..	1	W.S.	*Eucalyptus piperita-Angophora costata.*	March.
	2	P.H.	*Eucalyptus pilularis-Angophora costata.*	May.
Epacris microphylla ..	1	W.S.	*Hakea teretifolia.*	March.
Epacris pulchella ..	1	W.S.	*Eucalyptus punctata-E. haemastoma-E. gummifera.*	March.
Monotoca elliptica ..	1	O.B.D.	*Leptospermum attenuatum.*	March.
	2	O.B.D.	*Eucalyptus pilularis.*	March.
	3	W.S.	*Eucalyptus piperita-Angophora costata-Syncarpia glomulifera.*	March.

‡ Locality abbreviations: N.P. = National Park; O.B.D. = Ocean Beach Dune Series; W.S. = Warrah Sanctuary, Pearl Beach District; B. = Berowra; K.C. = Kuring-gai Chase; P.H. = Pennant Hills; J. = Jannali.

for the lower nitrogen content of these species as compared with the other representatives of their families. With the exception of *A. suaveolens*, which bears phyllodes, the other species mentioned in Table 14 have true leaves and all of these exhibit much the same degree of lignification.

Shields (1953) reports that the total nitrogen content of mature leaves from dicotyledons growing in gypsum sand having a maximum concentration of nitrite and nitrate of 8 p.p.m. ranges from 12,500 to 40,000 p.p.m. of the dry leaf weight.

For comparison it is of interest to note the analyses given by Parberry and Swaby (1942). The average total nitrogen content of mesomorphic species was as follows: grasses, approx. 20,000 p.p.m.; legumes, 20,000–40,000 p.p.m. Mitchell's (1936) and Tamm's (1951) figures for leaf material of deciduous tree species mostly exceed 20,000 p.p.m. nitrogen.

(ii) Wood.

Details of the nitrogen content of the wood of some of the species listed in Table 14 will be reported in a later publication.

(iii) Litter.

To complete the description of the communities, the litter phase is briefly mentioned here. Additional investigations of litter returns will be reported later.

Method.

In the forest communities it was found that the greatest percentage of leaf litter was made up of the relatively large leaves from the tree stratum. Usually two or more species of *Eucalyptus* grow in association, and identification of individual fallen leaves to the various species, so that comparison of fresh and fallen material can be made, is frequently difficult. However, it was found that wherever *Angophora costata* was growing, a very considerable percentage of the leaf litter was composed of this species whose leaves can be recognized. Therefore separate nitrogen analyses were made on *Angophora* litter.

The samples were collected on fine wire frames raised two inches above ground level to allow evaporation of moisture from condensation and rain.

Results and Discussion.

To enable direct comparison of litter with fresh leaf material, results were expressed on an area as well as a dry weight basis (Table 15). This would eliminate errors due to loss of dry matter at the time of leaf fall or later. However, a comparison of litter

TABLE 15.

Concentration of Total Nitrogen in Angophora costata *Leaves.*

Month of Sampling.	Period Since Previous Sample.	Total Nitrogen (on Oven Dry Weight) (p.p.m.).	Total Nitrogen (Per sq. cm. of Leaf) (μg.)
Litter:			
November	4·0 months	3600	64
April	2·5 ,,	4300	78
September	1·0 ,,	6700	105
Fresh mature leaf:			
July (site: National Park) ..	—	6300	103
November (site: Kuring-gai) ..	—	7500	106

and fresh leaf figures in Table 16 indicates that no loss of dry matter does occur; in fact, a shrinkage in surface area of the litter might be suggested, but it is necessary to account for up to 27% of the original area if the variation between extreme values of g./sq. cm. in leaf and litter is due to shrinkage alone. Leaf thickness would need consideration also.

The litter analyses indicate that, at least for *Angophora* which forms the greatest percentage of litter in forest communities, nitrogen is not withdrawn into the plant before leaf fall.

TABLE 16.

Dry Weight of Angophora costata *Leaves.*

Details of Sample.	Oven Dry Weight of Leaves (g./sq. cm.).
Leaf litter. Site : Warrah Sanctuary.	
Month of Sampling :	
July–November	0·016
November–January	0·022
January–April	0·020
April–August	0·021
August–September	0·018
September–October	0·021
March–May	0·020
May–July	0·017
July–November	0·020
Mature fresh leaves :	
National Park—July	0·017
Kuring-gai—November	0·014

Fraser (1948) found that the nitrogen content of the undecomposed layer of *Casuarina* litter also was very similar to that of the fresh material, both when expressed on a dry weight and on a corrected ash basis.

TABLE 17.

Concentration of Nitrogen in General Litter Samples from Dry Sclerophyll Forest.

Samples collected at fortnightly intervals from May to December and bulked for final analysis.

Litter Sample.	Total Nitrogen (p.p.m.).
Leaf	4300
Twig	2900

All species may not be similar in this respect, however. This is suggested by the lower figure of 4300 p.p.m. for the bulked leaf sample composed of several species in Table 17. It would seem unlikely that loss by leaching before the samples were collected would account for this lower value, in view of the *Angophora* data.

TABLE 18.

Total Nitrogen Content of Mature Fruit and Seed.

Species.	Total Nitrogen (p.p.m.).		Nature of Seed.
	Fruit.	Seed.	
Proteaceae :			
Isopogon anemonifolius (Salisb.) Knight..	1,100	2,700	Furry, small.
Myrtaceae :			
Eucalyptus piperita	2,200	3,300	Minute.
Leptospermum squarrosum	2,200	7,000	Minute.
Leguminosae :			
Acacia linifolia (Vent.) Willd.	4,700	28,700	Very large ; 29/g.
Dillwynia ericifolia	—	33,100	Large ; 200/g.
Casuarinaceae :			
Casuarina distyla	3,100	33,000	Winged, small.
Epacridaceae :			
Seed of *Epacris pulchella* is extremely fine. The sample was a mixture of fruit pods and seed and contained 8,200 p.p.m. total nitrogen. With the exception of the Leguminosae and Epacridaceae species listed, whose fruit are leathery, the other species have woody fruit.			

Unless the differences in nitrogen content of the litter given in Table 15 are influenced by seasonal variation, it would appear that at least part of the nitrogen is leached fairly rapidly, since only approximately 60% remained after four months under conditions where natural decomposition would have been retarded.

In addition to leaf and twig litter (Table 17), flower, fruit and seed litter also require consideration. As in leaf material, the Leguminosae and Casuarinaceae show a much higher nitrogen content in their seed than the other species analysed (Table 18).

General Discussion.

In view of the illustration given above, of the deficiencies of phosphorus and nitrogen in these plant communities, the following points are worthy of comment.

The native vegetation forms a moderately dense cover represented by heath, scrub and forest. With the low initial mineral content of the parent material, such development is remarkable.

It would appear that considerable economy has been exercised to prevent the loss of nutrients from the communties and maintain the original "working capital" (Beadle and Burges, 1949) of bases and nitrogen. In this regard, analyses of drainage waters and a tracing of root systems, especially of tree species and denitrification studies, should prove particularly illuminating. From observations of Beadle (private communication) and Hannon (Table 3 and unpublished data), the loss of phosphorus and net loss of nitrogen in the fire-free communities is not detectable. From her studies of *Casuarina* litter, Fraser (1948) has suggested the occurrence of a calcium cycle in these communities. Turner (1954), in preliminary work on the composition of eucalypt forest litter, has also noted that the calcium and potassium content of the leaf litter in dry sclerophyll forest communities exceeds that in wet sclerophyll. The phosphorus value is much lower. The ecosystem may well be regarded as a closed cycle, apparently with a comparatively low metabolic rate, yet with an efficiency approaching 100%.

In addition, the species have been selected for, or adapted to, the conditions of low water and nutrient supply. Analytical data (Table 14) show their nitrogen content to be extremely low. Beadle's (1954) figures for phosphorus are correspondingly low.

Further physiological investigations of representatives of the flora would be of great value. As mentioned before, studies on the *Eucalyptus* litter decomposition and the nature of the soil organic matter and microflora would be of interest also.

The means by which nitrogen has reached its present level calls for attention. It has been shown that the total nitrogen content of these soils is low, but quite comparable with similar soils; but the carbon-nitrogen ratio is higher and available nitrogen lower than in other parts of the world. This suggests that the rate of nitrification of organic matter will be low.

As previously mentioned, the sources of nitrogen for natural plant communities have not received careful investigation. The major contributing factors as symbiotic and non-symbiotic nitrogen fixation are well known and it has been usual to deduce, by inspection of the occurrence of legumes, nitrogen-fixing algae or bacteria, which agent was responsible for nitrogen accessions. The analyses of leguminous and *Casuarina* tissue (Tables 14 and 18) suggest that they have an independent supply of nitrogen. The role that they have played in building up the nitrogen content of these communities to their present level might well be of importance. Studies on the development and circulation of nitrogen in the Hawkesbury Sandstone communities will be reported later.

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EXPLANATION OF PLATE X.

Native species growing in Hawkesbury Sandstone soil under various nutrient treatments.

A: *Acacia suaveolens* (Sm.) Willd.
Left to right: 1–3 Eucalypt forest soil
1: + Water; 2: + P; 3: + P + N
4–6 Shrub swamp soil
4: + Water; 5: + P; 6: + P + N

B: *Casuarina littoralis* (Salisb.) (*C. suberosa* Ott. & Dietr.).
Left to right: 1–3 Shrub swamp soil
1: + P + N; 2: + P; 3: + Water
4–6 Eucalypt forest soil
4: + Water; 5: + P; 6: + P + N

C: *Eucalyptus gummifera* (Gaertn.) Hochr.
Left to right: 1–3 Eucalypt forest soil
1: + Water; 2: + P; 3: + P + N
4–6 Shrub swamp soil
4: + Water; 5: + P; 6: + P + N

D: *Hakea dactyloides* (Gaertn.) Cav.
Left to right: 1–3 Shrub swamp soil
1: + P + N; 2: + P; 3: + Water
4–6 Eucalypt forest soil
4: + Water; 5: + P; 6: + P + N

Reduction: × 0·05 approx.

Photographs by Mr. J. D. McLean.